Pacific Science (1978), vol. 32, no. 2

Diel, Lunar, and Seasonal Periodicity in the Reproductive Behavior of the Pomacanthid Fish, *Centropyge potteri*, and Some Other Reef Fishes in Hawaii[1]

PHIL S. LOBEL[2]

ABSTRACT: The reproductive behavior of five Hawaiian coral reef fishes are described for the first time: an angelfish (Pomacanthidae), three butterflyfishes (*Chaetodon fremblii*, *C. multicinctus*, *C. unimaculatus*), and a goatfish (*Parupeneus multifasciatus*). The angelfish, *Centropyge potteri*, was examined in detail. It was determined that every month from December until May it spawns each evening during the week preceding a full moon. On extensive coral reefs *C. potteri* occurs mostly in pairs, whereas on patch reefs a single male may control access to several females. Thus, males on patch reefs seem to enjoy greater reproductive success than males on extensive reefs. The advantages potentially associated with spawning synchronized at dusk between the first quarter and full moon primarily involve reduced mortality of offspring. The annual reproductive period, which is shared by several other Hawaiian shore fishes, is correlated with a semiannual shift in ocean currents that may retain larvae in the vicinity of the Hawaiian reefs at that time.

REPRODUCTIVE BEHAVIOR OF MARINE FISHES has been scarcely described for any but a few taxa (Breder and Rosen 1966), e.g., some pomacentrids (Clarke 1970, Helfrich 1958, Myrberg, Brahy, and Emery 1967, Sale 1971, Stevenson 1963, Swerdloff 1970, Walters 1967) and some labrids and scarids (Potts 1974, Randall and Randall 1963, Reinboth 1973, Roede 1972, Youngbluth 1968). Despite numbers field studies, the reproductive activities of many reef fishes remain unknown. Most observations on the activity of reef fishes have been during midday and thus have missed peaks of reproductive activity at dusk, where and when such peaks occur. A similar situation existed with predatory activities until observations were made during the crepuscular periods (e.g., Hobson 1965, 1968, 1972, 1974). This article reports the spawning behavior and periodicity of a pomacanthid, *Centropyge potteri*, which spawns at dusk. Also included are observations of other species that spawn at the same time, notably three chaetodontids, one mullid, and three acanthurids.

METHODS

Direct Observations

Fishes were watched under water using scuba equipment during approximately 300 hr at all times of day and night, including 30 hr immediately before sunset, from June 1974 to June 1975. I soon recognized that the reef fishes were spawning predominantly during dusk. To minimize the influence of my presence on this activity, I positioned myself on station at least 30 min before the fish began courtship. The sudden appearance of a diver (or a large fish) caused many fishes to cease spawning activity. I remained on station until convinced that all activity had ceased and that the fishes had retired for the night [for approximate timing of various species, see Hobson (1972)]. Spawning activ-

[1] Manuscript accepted 11 February 1978.

[2] University of Hawaii, Department of Zoology, Honolulu, Hawaii 96822. Current address: Harvard University, Museum of Comparative Zoology, Cambridge, Massachusetts 02138.

TABLE 1

SIZE AND RATIO OF THE SEXES OF *Centropyge potteri* ON PATCH REEF AREAS

LOCATION	DEPTH (m)	NUMBER OF FISH SAMPLED	NUMBER, MALE:FEMALE	RATIO, MALE:FEMALE	STANDARD LENGTH, MEAN AND RANGE (mm)	PATCH HABITAT
Outside Kaneohe Bay (Oahu)	16	14	3:11	1:3.67	76.5 (61–87)	Fish from two rubble areas 2 meters apart; total area approximately 24 m^2
Waikiki (Oahu)	8.3	4	1:3	1:3	76.5 (63–91)	Solitary coral cluster approximately 3 meters from extensive reef; patch approximately 1 meter diameter
	16–20	7	1:6	1:6	65 (45.5–83)	Three rocks, 0.6 meter at greatest length; close together with scattered rubble
	20	8	2:6	1:3	76 (61–94)	Three rocks, 1 meter at greatest length; spaced 1 meter apart with rubble around
	25–30	5	1:4	1:4	63 (54–68)	Single coral cluster 1.4 m^2, 0.6 meter high
	25–30	7	1:6	1:6	71 (59–89)	Patch of large rock rubble approximately 16 m^2
Totals	8.5–30	45	9:36	1:4.28 $\pm$ 1.39	71 (45.5–94)	

NOTE: The difference between sex ratios between patch and extensive reefs (Table 2) was significant (t statistic, two-tail level of significance; $0.01 < P < 0.02$).

TABLE 2

SIZE AND RATIO OF THE SEXES OF *Centropyge potteri* ON EXTENSIVE REEF AND RUBBLE HABITATS

LOCATION	DEPTH (m)	NUMBER OF FISH SAMPLED	NUMBER, MALE:FEMALE	RATIO, MALE:FEMALE	STANDARD LENGTH, MEAN AND RANGE (mm)	EXTENSIVE REEF AND RUBBLE HABITAT
Mahukona (Hawaii)	11–16	26	12:14	1:1.17	62 (47–81)	Extensive reef with dense layers of coral including *Porites lobata*, *Porites compressa*, *Pocillopora meandrina*
Makaha (Oahu)	8.3–16	12	4:8	1:2	57.5 (38–71)	Vast area of large rubble on top and below a ledge
Makua (Oahu)	8.3–10	10	6:4	1:0.67	66 (55–81)	Large cave surrounded by rubble and coral; total area approximately 67,000 m^2
Moanalua Bay (Oahu)	8.3–13	18	6:12	1:2	75 (51–98)	Scattered corals, mostly *Pocillopora meandrina*, and large rubble spaced less than 1 meter apart
Waikiki (Oahu)	16–30	58	24:34	1:1.42	73 (42–95)	Large rubble covering vast areas; rubble in some patches, but less than 1 meter part; very little live coral
Wreck buoy	8.3–10	50	20:30	1:1.5	77.5 (49–101)	Extensive region of large corals, mainly *Porites lobata* and *Pocillopora meandrina* corals spaced less than 1 meter apart
Totals	8.3–30	174	72:98	1:1.46 $\pm$ 0.51	68.5 (38–101)	

NOTE: See note for Table 1.

TABLE 3

DIRECT OBSERVATION OF *Centropyge potteri* SPAWNING, 1975

DATE OF FULL MOON	DATE OF OBSERVATION	REEF TYPE	NUMBER OF FISH SEEN SPAWNING
27 January	25 January	Extensive	Six pairs
26 February	25 February	Patch	One male and six females, male spawned with
27 March	22–26 March	Patch	three or four of six females each evening
25 April	19 April	Patch	One male and three females
	20–24 April	Extensive	Eight pairs spawned each evening
23 June	21 June	Extensive	One pair out of eight spawned

NOTE: All spawning occurred within 1 hr of sunset. Each female spawned once, although where more than one female was available, males spawned more than once. A total of 7 harem and 31 pair spawnings were observed (a pair spawning refers to a single spawning by a male with one female; a harem spawning refers to one male spawning repeatedly with two or more females).

ity was not observed during the several dives at sunrise.

Study Areas

Study sites were located primarily on the reefs off Waikiki and the Waianae coast, Oahu Island, and the Kona coast, Hawaii Island. These reefs were typically composed of stony corals (*Porites* spp. and *Pocillopora* spp.) and rubble. Species composition of comparable regions has been reported by Hobson (1974).

Weights and Measures

Specimens were collected by spear. All weights were assessed on a Mettler electronic balance. Fishes were generally examined while fresh or frozen. Percentage gonad weight was determined by dividing the blot-dry gonad weight by the blot-dry total body weight of a fish and multiplying by 100. A total of 315 specimens of *Centropyge potteri* were examined.

Definitions

Reefs inhabited by *Centropyge potteri* were classified as either extensive or patch reefs. A patch of rock/coral with an area of less than 24 m^2 (the largest patch reef found), surrounded by sand, and at least 100 meters distant from neighboring reefs is defined as a patch reef. Patches near other reefs are defined as satellite reefs. Extensive reefs are characteristic of areas usually associated with the notion of coral reefs, a vast expanse of coral and rubble.

Terms such as abundant, common, occasional, and rare are used as defined by Chave and Eckert (1974).

HABITAT EFFECT ON SEX RATIO

Adult *Centroyge potteri* inhabit reefs consisting of large corals and boulders within the 3- to 50-meter depth range. In such areas, this species is among the ten most frequently seen fishes (Hobson 1974).

The ratio of males to females differed between patch reefs and extensive reefs. There were approximately two to four more females per male on a patch reef than on extensive reefs (Tables 1, 2). This differential availability of females was evident during reproduction. Males on patch reefs spawned with each female, one at a time consecutively per evening, whereas males on extensive reefs did not spawn with more than one female per evening (Table 3).

The basis for these differing sex ratios has not been thoroughly tested; however, there were indications that it may be related to male defense of a spawning site. The most important aspect of such territory appears to be a towering rock or coral knoll over which the fish spawn (see details below). I introduced foreign males onto patch reefs on five occasions and each time the resident male attacked and kept the intruder over the sand beside the patch reef. Presumably it is dangerous for the fish to travel between reefs.

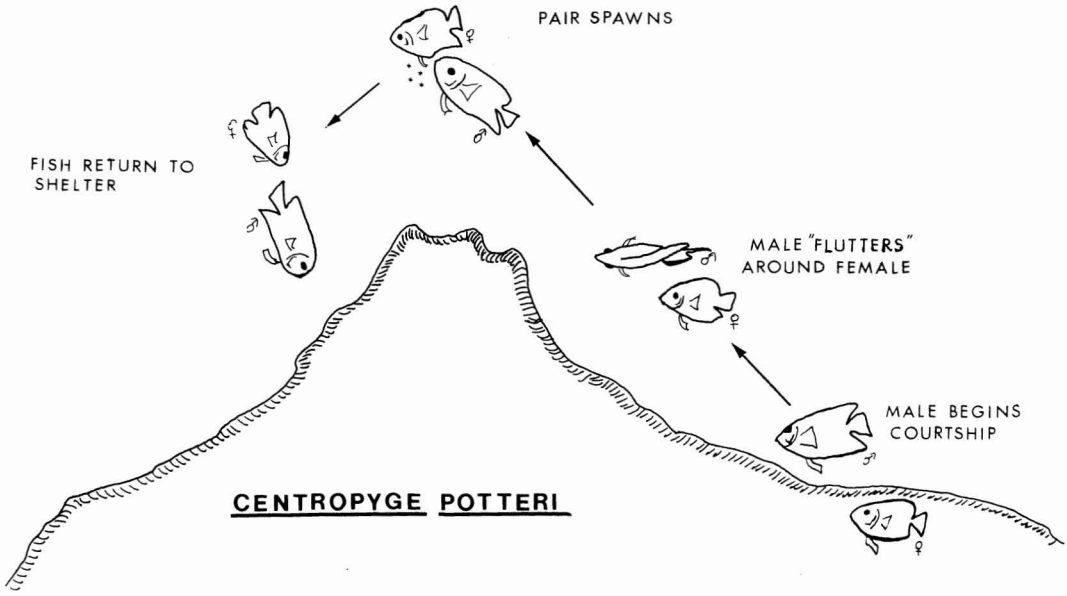

FIGURE 1. Generalized courtship and spawning sequence.

The attacks by the resident were most persistent during the time of reproduction. *Centropyge potteri* is a herbivore and did not defend the territory against other species with similar food habits. During 20 hr of observation at midday only four agonistic encounters occurred between *C. potteri* and *Ctenochaetus strigosus* (Acanthuridae) and *Eupomacentrus fasciolatus* (= *Pomacentrus jenkinsi*, Pomacentridae). In the extensive coral reef habitat the availability of spawning sites, by inspection, was greater than on patch reefs, perhaps allowing more males to occupy spawning sites and giving females a broader choice of mates or merely reducing the ability of any one male to exclude other males from the large reef (see description of spawning site below). Individuals limit their movements to restricted, well-defined locations (Hobson 1974).

SPAWNING BEHAVIOR OF *Centropyge potteri*

The following generalized description of *Centropyge potteri* spawning is based upon 31 observations of pair spawning and 7 harem spawnings (Table 3). One sequence has been entirely recorded on super-8 mm movie film. The general sequence of behavior is presented diagramatically in Figure 1.

Courtship was initiated by the male, who ceased feeding and began courting about 1 hr before sunset. The male swam toward a female in a vertical undulating style distinct from normal swimming motion. He stopped above her and erected all median fins while fluttering the pectoral fins. This display continued as the male drifted slowly upward with his head diagonally up or with his side parallel to the substrate. If the female failed to follow, the male halted immediately and darted back to her. The male continued courtship by swimming around the female in the undulating fashion. In this way, the male approached the female as he swam forward while rising and dropping in a swooping, fluttering motion. Courtship continued until the female was enticed over to the prominent coral or rock tower and she rose above the tower with the male. This usually only required a few courting passes. Spawning occurred only over the tallest coral or rock in the immediate area. During courtship and spawning the overall blue color of both fish paled as the red color intensified.

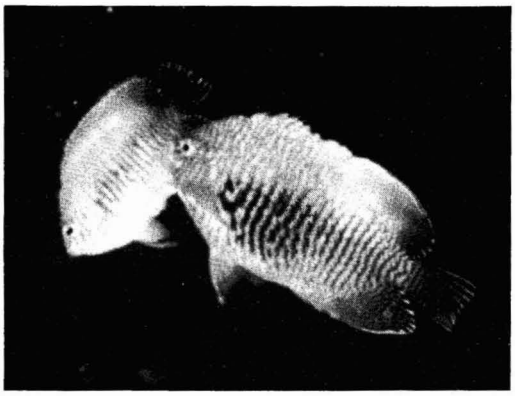

FIGURE 2. *Centropyge potteri* during the climax of spawning. The male is the larger individual on the right.

During the first few encounters, the female rose up with the male and then darted back to cover when the male attempted to move to the spawning position. The male pursued her while continuing his courtship display. Spawning climaxed when the female remained in midwater, about 1 meter above the coral/rock tower. The male approached from underneath and appeared to press his snout against her abdomen (Figure 2). Such contact may signal or facilitate egg release. A single burst of eggs was broadcast. Because of the low light level I could not see sperm released in the field, but in aquaria spawnings of related *Centropyge fisheri* it occurred simultaneously with egg release. Immediately after release of eggs and sperm, the pair darted to cover with the female chasing the male, apparently nipping at his caudal fin. Chasing by the female happened only after consummation of the spawning act and not during earlier episodes of courtship. Spawning was consummated before sunset, but the absolute time varied. Soon after sunset the fish retired into a cavity in the reef for the night.

During courtship various sounds, like clicks and grunts, were produced by these fish, although their precise role during reproduction was not examined.

Similar reproduction behavior was noted in aquarium spawnings of *Centropyge bispinosus* (Bauer and Klay 1974, Lobel 1975), *C. fisheri; C. flavissimus* spawned likewise during the full moon period of May 1975 at Enewetak Atoll, Marshall Islands.

REPRODUCTIVE PERIODICITY

The peak reproductive season for *Centropyge potteri* began in December and continued through May (Figure 3). Development of the gonad within this annual season was correlated with the full moon; the female's ovary attained its greatest weight before spawning commenced—about 1 week before the full moon (Figure 4). *Centropyge potteri* was observed to spawn only during the week preceding the full moon from January to April 1975 (Table 3). No observation dives were performed during the full moon period of May 1975. In June 1975, however, three dives during the full moon week revealed only one spawning event, although nine other pairs were in full view. Observation during other evenings of the lunar cycle and other times of the year gave no indications of spawning having occurred.

The question whether spawning occurs during the months of June to December may still be debated. However, it is evident that if spawning does occur at that time, the size of spawn will be very much less than during the months of December through May. The one male seen spawning in June did so only once, although he pursued two neighboring females that fled rather than respond to courtship. If spawning does occur during the off-season, it is probably infrequent.

SPAWNING BEHAVIOR OF CHAETODONTIDS

During the observations of *Centropyge potteri*, spawning was observed coincidentally in three species of chaetodontids: *Chaetodon fremblii*, *C. unimaculatus* (three observations of each), and *C. multicinctus* (six observations). All spawned within the hour preceding sunset during the week before the full moon, February and March 1975.

The reproductive behavior of *C. multicinctus* appeared typical. Although more than two fish were present, only pairs

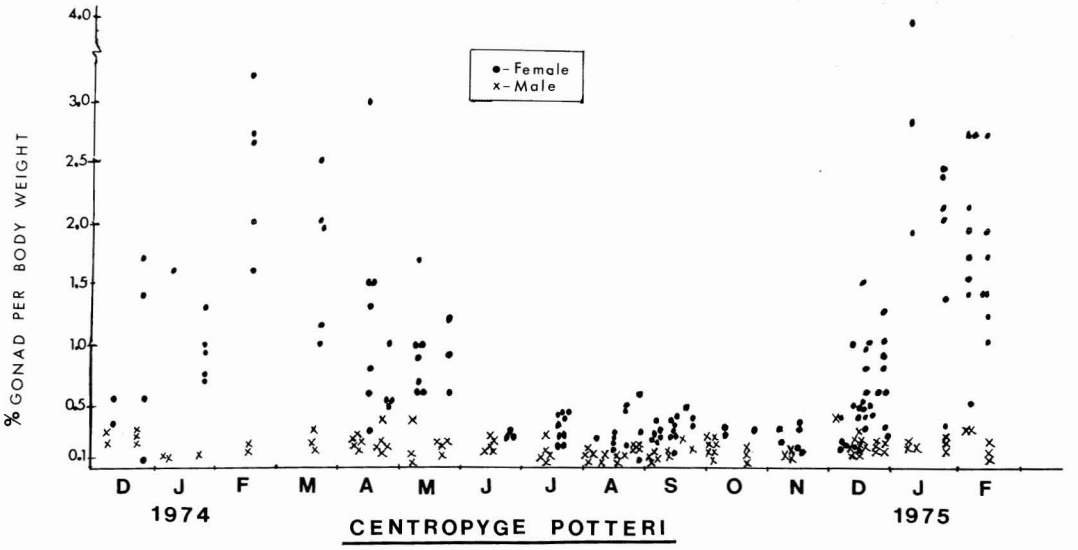

FIGURE 3. Annual reproductive season. Percentage gonad weight for *Centropyge potteri* from December 1973 through February 1975, indicating a peak reproductive season beginning in December and ending in June.

spawned. When spawning, *C. unimaculatus* and *C. fremblii* occurred solely as pairs. Aggregations of spawning *C. multicinctus* consisted four times of four individuals and two times of three individuals. One group of four *C. multicinctus* apparently included at least one female and two males. I did not spear any fish so that my actions would not disturb the behavior sequence. Female chaetodontids, obviously swollen with roe, led the group or pair as they swam along the reef. The sex of an individual was determined by observation as it spawned. Courtship among chaetodontids was less elaborate than among *Centropyge potteri.* As the chaetodontids swam along the reef, the female tilted her head slightly downward as she continued in front of the male. The male swam from behind and up alongside the female. As the male reached the female and placed his snout to her abdomen, both fish quivered and eggs and sperm were released (Figure 5). In one case, a male *Chaetodon multicinctus* approached a female in this fashion three times before spawning. The chaetodontid spawning posture was strikingly similar to that described for *Centropyge potteri.* Again, the nuzzling by the male may signal the female to release eggs. *Chaetodon multicinctus* and *C. unimaculatus* rose up approximately 0.5 meter above the substrate to spawn. *Chaetodon fremblii* rose into the water between 1 and 2 meters when it spawned.

At midday during the week before the full moon of May 1975 at Enewetak Atoll, Marshall Islands, a pair of *Megaprotodon trifascialis* were filmed in a brief encounter that culminated with the assumption of the spawning position, but spawning did not occur. *Megaprotodon trifascialis* are solitary territorial fish with males and females residing on neighboring *Acropora* sp. corals (Reese 1973).

Forcipiger flavissimus was also sighted in the chaetodontid spawning position although actual spawning was not seen. The position differed slightly because of the long snout. The male nuzzled with his forehead and kept his snout underneath. This single observation was made during the hour before sunset, 23 March 1975 (4 days before the full moon).

SPAWNING BEHAVIOR OF A MULLID

The mullid *Parupeneus multifasciatus* was sighted spawning four times at dusk on 25 March 1975, 2 days before the full moon.

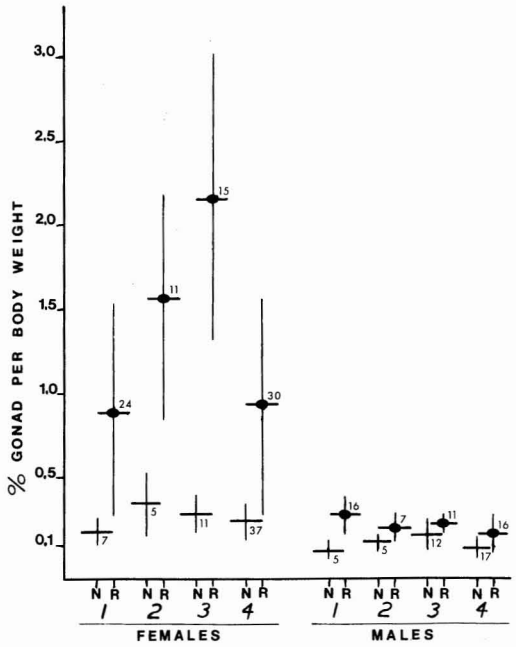

FIGURE 4. Lunar periodicity of gonad development: N indicates individuals collected during the nonreproductive season; R indicates individuals collected during the reproductive season, December through May. Total number of fish studied was 140 females and 89 males; the number beside each symbol indicates the number in the sample. *1* = fish collected 1–7 days after the full moon; *2* = fish collected 8–14 days after the full moon; *3* = fish collected 15–23 days after the full moon; *4* = fish collected 24 days after and up until the next full moon.

An aggregation of approximately ten fish hovered about 1 meter above a sandy area next to a reef at 10 meters depth. The largest member, most probably the male, was a darker color than the others and darted conspicuously around and through the aggregation until another fish joined along its side. The pair ascended, side by side, to the surface, where they spawned while swimming forward just beneath the surface. After spawning, they separated and returned to the reef, whereupon I lost sight of them. This mullid was the most difficult of all fish to approach. When I came within 5 meters they ceased all spawning activity. In contrast, I was able to get within 1 meter of spawning *Centropyge potteri* and within 2 meters of the chaetodontids.

Randall and Randall (1963) also reported upward movement leading to spawning and large aggregations for the Caribbean mullid, *Parupeneus maculatus*.

SPAWNING BEHAVIOR OF ACANTHURIDS

Three species of acanthurids spawned during the same time period as the previously described fishes during March and April 1975. A small aggregation of about a dozen individuals swam together until they suddenly darted upward a few meters, spawned

FIGURE 5. *Chaetodon multicinctus* spawning. The female on the farthest right with a male behind. The sex of the third individual is not known.

and descended in unison. I noted several such group spawnings of *Acanthurus nigrorus*, *Ctenochaetus strigosus*, and *Zebrasoma flavescens*. Their reproductive behavior did not differ significantly from the reproductive behavior of acanthurids as described by Randall (1961*b*).

DISCUSSION

The schedule of reproduction among Hawaiian reef fishes reflects adaptation to a variety of ecological factors. Diel periodicity appears to be influenced primarily by the balance between the threats of diurnal planktivores feeding on eggs and newly hatched larvae and crepuscular piscivores attacking spawning adults. Spawning at dusk involves minimal risk to eggs and larvae, but it is the time of peak predation upon adult fishes. Lunar reproductive synchrony further reduces the probability of predation on individuals by creating a swamping effect [the selfish herd hypothesis, see Reaka (1976)]. The tide is outgoing during evenings shortly before a full moon and may aid in removal of eggs and larvae from the immediate vicinity of the reef where they are exposed to reef planktivores. The annual peak in reproductive activity is correlated with a shift in ocean current that retains pelagic larvae around the islands and ensures their return to Hawaiian reefs. These various factors exert their influence at different times (diel, lunar, and annual) and result in selection for reproductive cycles that overlap in many ways. Their relative effects on timing, however, are probably not as distinct as the categories presented below might imply.

Reproductive Behavior and Coloration

Pomacanthids and chaetodontids exhibited similar reproductive behavior and a mating position that is unlike other fishes whose behavior has been described. One difference between chaetodontids and pomacanthids is that the chaetodontids did not restrict their activity to specific locations on the reef. Whereas *Centropyge potteri* always spawned over the same spot and courtship was directed toward enticing a female to a specific tall rock/coral in the immediate territory, chaetodontids spawned wherever they might be in a general home range without apparent orientation to specific reef structures. Spawning did, however, take place on the seaward side of the reef. Reese (1975) has described other aspects of chaetodontid behavior. The taxonomic relationship of the Pomacanthidae and Chaetodontidae has been reviewed by Freihofer (1963) and Burgess (1974).

It is well known that chaetodontids, like many other fishes, transform into nocturnal colorations. Although the full significance of these nocturnal colors remains uncertain, the fact that chaetodontids wait until dusk to spawn agrees with Hobson's (1974) contention that recognition is important during both day and night. Hobson (1974) suggests: "It is logical that diurnal fishes would employ visual clues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona (Hawaii) tend to accentuate a contrast, thus making them more visible at lower light levels. Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display" (p. 1022). Since at least three species spawn during dusk, these low-light-level, color-contrasting displays may aid in mate recognition. Probably the situation is similar in other species that change color when spawning at low light levels. Although, I noted color changes in these fishes when they spawned at dusk, I am not familiar enough with their nocturnal colorations to evaluate the similarities.

Diel Reproductive Periodicity

Diurnal planktivores are adapted for plucking small prey from midwater, while nocturnal planktivores, such as apogonids

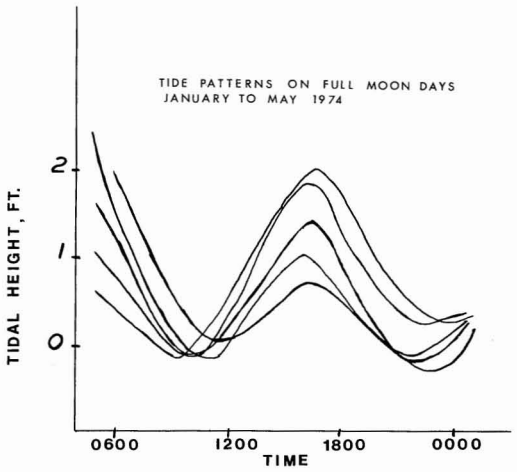

FIGURE 6. Tide patterns during the full moon of the months January until May 1974. These patterns are representative, showing the general retreating tide in the evening and a morning increasing tide.

and some holocentrids, possess large mouths and feed mainly on large plankton prey (Hobson 1974, Hobson and Chess 1976). By dusk, most diurnal planktivores have descended to the reef for the night (Collette and Talbot 1972, Domm and Domm 1973, Hobson 1972). Spawning at dusk may reduce the probability of eggs being eaten in two ways: (1) there are few active planktivores and (2) any planktivores that are still active may be quickly satiated by the simultaneous spawning by many fishes. In addition, there was an outgoing tide during the time of spawning of this study, which may aid in sweeping eggs and larvae from the reef and from the grasp of planktivores that are still active (Figure 6). At this time the difference in the height of the tide from high to low was greatest, which may influence the rate of flow. In the mornings the tide was incoming.

The reproductive activity of broadcast-spawning species was not evident in the reef areas where there were planktivores or other species spawning. The avoidance response by spawning fishes to planktivores has also been reported by Hobson (1965). Twilight is a visually difficult time for most reef fishes and is when predation is at its peak (Hobson 1972, 1974, Munz and McFarland 1973). It may be that the low level of reflected moonlight combined with sunlight just before sunset is sufficient for fishes to recognize mates, spawn, and also avoid potential predators, but is not enough for planktivorous fishes, requiring high visual acuity, to continue foraging.

The threat from predators may partially explain why a prominent reef structure towering in the home range of *Centropyge potteri* is important. While spawning in midwater, they were still close to a reef shelter to which they darted between encounters, after spawning, and when disturbed by other fishes. Similar orientation to a tall reef structure has been reported for *Hypoplectrus chlorurus* (Serranidae) when spawning (Barlow 1975).

The importance of such a towering coral/rock is evident on patch reefs, where it may be one factor limiting the number of spawning males. A male on a patch reef controlled a limited area and consequently access to resident females, while mostly pairs occurred on extensive reefs. Since females spawn only once nightly, the males on patch reefs very probably enjoy a greater reproductive success. This aspect of the biology of *C. potteri* should be further examined experimentally.

Spawning during the daytime is known to occur among some pomacentrids, labrids, and scarids (Helfrich 1958, Meyer 1977, Moyer 1975, Moyer and Bell 1976, Potts 1974, Reinboth 1973, Roede 1972, Sale 1971, Youngbluth 1968). Pomacentrids protect their nests against predators, and labrids and scarids release large numbers of eggs. Active predation of labrid eggs by planktivorous pomacentrids has been described by Meyer (1977). Eggs may be less likely to be eaten if they are toxic [as is known only for some tetraodontiform fishes and a cottid, Pillsbury (1957)] or float at the water's surface where few fishes feed. The eggs of some nesting pomacentrids and balistids hatch predominantly during the dark (Allen 1972, Lobel and Johannes 1977). The eggs of the pomacentrid *Amphiprion clarkii* hatch between 34 and 70 min after sunset (Moyer and Bell 1976). These fishes would also share the advantages of fishes spawning at this time.

TABLE 4

FISHES WITH PELAGIC LARVAE SHOWN TO HAVE A PEAK SPAWNING SEASON BETWEEN DECEMBER AND JUNE IN HAWAII

FAMILY	SPECIES	AUTHORITY
Acanthuridae	*Acanthurus triostegus sandvicensis*	Randall 1961*a*
Blenniidae	*Entromacrodus marmoratus*	Strasburg 1953
	Istiblennius zebra	Strasburg 1953
Chaetodontidae	*Chaetodon miliaris*	Ralston 1975, 1976
Engraulidae	*Stolephorus purpureus*	Leary, Murphy, and Miller 1975
Kuhliidae	*Kuhlia sandvicensis*	Tester and Takata 1953
Labridae	*Labroides phthirophagus*	Youngbluth 1968
Muraenidae	*Gymnothorax eurostus*	Gosline and Brock 1960
Pomacanthidae	*Centropyge potteri*	This study
Pomacentridae	*Abudefduf abdominalis*	Helfrich 1958
	Chromis ovalis	Swerdloff 1970
	Chromis verator	Swerdloff 1970
	Dascyllus albisella	Stevenson 1963
	Eupomacentrus fasciolatus (= *Pomacentrus jenkinsi*)	Gosline 1958

NOTE: This table lists only those species with pelagic larvae. Spawning has been said to occur throughout the year in many of these fishes; however, all have been reported with *peak* reproductive seasons at this time. Details will be presented elsewhere (Lobel and Reaka 1977). All species listed are endemic to Hawaii except *G. eurostus* and *E. fasciolatus*.

Lunar Reproductive Periodicity

Annual and lunar spawning seasons have been described for many temperate zone fishes (e.g., Schwassman 1971), but reports on the spawning periods of tropical fishes are scattered and few.

In the Society Islands, *Ctenochaetus striatus* and *Zebrasoma scopas* spawned at dusk within 5 days preceding the full moon, and *Acanthurus triostegus sandvicensis* also spawns on a lunar cycle (Randall 1961*a*, *b*). Randall and Randall (1963) suggested that spawning occurred for *Scarus rupripinne* (Sacridae) during the full moon and possibly during the new moon in the Caribbean Sea. Roede (1972) reported that peak reproductive activity for seven Caribbean labrids was pronounced at the full moon. She also found two other lower peaks during the lunar month, and she suggests that propagation in these labrids may continue throughout the month but with increased activity during the full moon period. *Abudefduf abdominalis* (Pomacentridae) spawned during full and new moon phases in Hawaii (Helfrich 1958), as does *Amphiprion* spp. (Pomacentridae) at Enewetak Atoll (Allen 1972). Allen (1972) reported 26 of 34 spawnings of *Amphiprion* spp. 6 days before or after the full moon, with 20 of 34 of the nests hatching within 1 week of the full moon. Two other pomacentrids also have spawning peaks on about the full moon (Moyer 1975, Moyer and Bell 1976). Johannes at Palau has determined full moon spawning synchrony for the nesting triggerfish, *Pseudobalistes flavimarginatus* (Lobel and Johannes 1977) Lunar periodicity has also been suggested for *Extremeus micropus* and *Gnathodon speciosus* (Carangidae) in Hawaii (Watson and Leis 1974). *Kuhlia sandvicensis* (Kuhliidae) is also suspected of spawning near the time of full moon in Hawaii (Tester and Takata 1953). In addition, many marine invertebrates are known to spawn during the full moon (Korringa 1947).

An explanation fully accounting for a peak period of spawning and hatching eggs during dusk on evenings of the first quarter to full moon is difficult to construct, however, several nonexclusive potential factors may be involved:

1. Reduced threat to eggs and larvae due to midwater planktivores which are generally inactive by dusk.
2. Eggs and larvae swept out to sea with retreating tide.
3. Lunar periodicity may act as a cue synchronizing simultaneous reproductive readiness within a species.

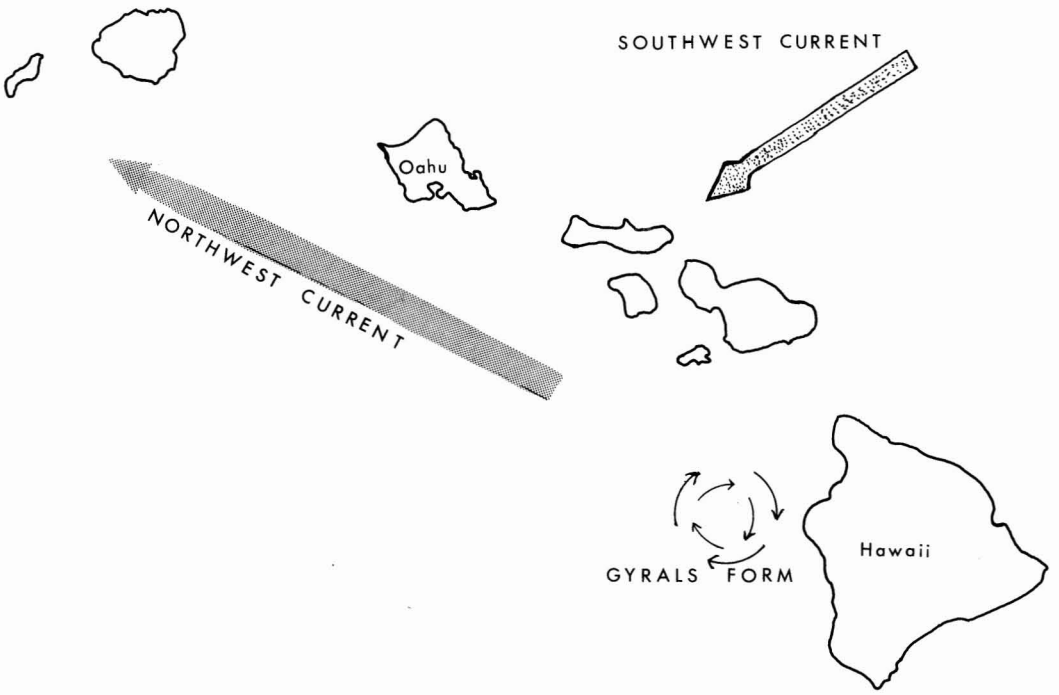

FIGURE 7. Generalized direction of ocean currents as interpreted from the data of Barkley, Ito, and Brown (1964). The northwest current with gyrals forming in the lee of the island of Hawaii occurs during the peak spawning season, December to June. The shift to the southwest current direction begins in June and lasts until December; eventually, it connects with the equatorial current (Jones 1968).

4. Lunar periodicity may serve to synchronize spawning of several species to create a swamping effect, quickly satiating any planktivores that may still be active.
5. Since most larvae are photopositive, the full moonlight may stimulate larvae to swim toward the surface, thus preventing them from settling back to the reef where they may be trapped and eaten (Allen 1972).

Annual Reproductive Periodicity

While tropical fishes are generally believed to spawn throughout the year, a spring spawning peak during February through April is evident among Caribbean reef fishes (Munro *et al.* 1973). My observations suggest that reproductive activity in several Hawaiian reef fishes also peaks in the spring from December until June (Table 4). During this period in Hawaii there were generally lower surface temperatures and salinities that correlated with an abundance of all species' eggs (Watson and Leis 1974). Water temperatures were also at their lowest during the reproductive peak in the Caribbean (Munro *et al.* 1973). Watson and Leis suggested that these physical changes in Hawaii reflect a shift in ocean currents and such a shift may increase the retention of pelagic eggs and larvae near the Hawaiian Islands (see also Jones 1968, Sale 1970). This is being further examined by Lobel and Reaka (1977) using the results of drift-bottle experiments by Barkley, Ito, and Brown (1964). Full moon phases during this season were associated with peak tidal changes and during this study spawning occurred at dusk, which coincided with an outgoing tide.

The seasonal change of ocean current direction has been assessed by the recovery of drift bottles released in the vicinity of the island of Hawaii (Barkley, Ito, and Brown 1964) (Figure 7). The current drift is roughly parallel to the Hawaiian Islands from January

until June. The direction begins to shift after June from the predominantly northwest parallel direction to a drift primarily to the southwest. This southwesterly current eventually becomes part of the north equatorial current (Jones 1968). The northwesterly current direction and effects of tidal changes that run parallel to the shore create pockets of eddies between the islands where larvae may accumulate. Additionally, surface current gyrals form in the lee of the island of Hawaii, the southernmost island in the Hawaiian Archipelago. These gyrals move along with the northwest current, and organisms trapped within may be easily transported along the island chain (Jones 1968). The effectiveness of surface current gyrals in trapping pelagic larvae has been suggested by the distribution of acanthurid larvae; Sale (1970) found larval acanthurids that were swept past an island every 5 to 6 days as a gyral rotated. Species with pelagic offspring dispersed into the ocean during the period June until December may have their progeny dispersed to the north equatorial current. Thus, they may not contribute significantly at that time to the repopulation of the Hawaiian fauna.

The changing seasonal current pattern may reflect the possibility for flow to be stronger and more westerly in July to December; however, a random component of flow may be predominant at any time (anonymous reviewer, personal communication). The variability in the seasonality of these patterns is not yet known. Even so, Lobel and Reaka (1977) show that the number of drifting objects lost from or retained in Hawaiian waters during the two seasons are statistically significantly different. Marjorie Reaka and I are presently evaluating the general applicability of the hypothesis for the fauna in Hawaii and elsewhere. The fact that 12 of the 14 species so far reported (Table 4) are taxonomically recognized Hawaiian endemics emphasizes the limited distribution of these fishes. Knowledge of how widespread this phenomenon is among Hawaiian aquatic animals requires considerably more data on the reproductive seasonality of both endemics and more widely ranging species.

The populations of reefs which are adapted to unique situations are confronted with the problem of conserving their pelagic stages contrary to dispersing larvae into the major ocean current systems. Since many reef animals possess a pelagic stage in their life history, this selection pressure may be widespread where we find organisms (1) restricted to specific environmental circumstance, (2) in specific and very isolated places such as Hawaii, and/or (3) in a situation where the results of competitive interactions depend upon a large number of recruits (e.g., Sale 1974, 1977). Synchronization of reproduction with ocean currents favoring return of larvae to home reefs may be one mechanism by which reduced dispersal is accomplished. If the different ecological setting in Hawaii favors natural selection of those taxa with a mechanism assuring return of larvae to suitable reefs, we may expect a peak reproductive season between December and June to be evident among those species especially suited to Hawaiian habitats. If this proves true, we may predict such seasonality at least among the recognized endemic species [29 percent of the fishes (Randall 1976; see also Gosline 1968)], which are among the most numerous on Hawaiian reefs.

ACKNOWLEDGMENTS

Many people generously aided me during my study while I was an undergraduate at the University of Hawaii. I am most grateful to George S. Losey and Leighton R. Taylor, who guided my research and study. My consistent diving companions helped not only in the field, but also in the interpretation of what we saw: Paul Allen, Paul Atkins, Joe Bauer, Sally Bauer, Ed Baughman, Deetsie Chave, John Earle, Denny Gorlick, Dan Johnson, Steve Ralston, and most especially Janie Culp. Ed Baughman and John Earle were also generous with the use of their boats. Research at Enewetak Atoll, Marshall Islands, was supported by the Mid-Pacific Marine Laboratory (S. V. Smith, Director). Equipment and laboratory space was provided freely by the Department of Zoology, the Hawaii Cooperative Fishery Unit, and the Waikiki Aquarium, University

of Hawaii. Interisland travel was made possible by Doug Pendleton, Marine Programs, University of Hawaii. I would also like to thank Edmund Hobson, John Randall, Marjorie Reaka, Ross Robertson, Peter Sale, and John Stimson for their aid and comments. Karen Cheng, Kathie Cunningham, and Arila Kourany kindly typed various versions of the manuscript. To all, my sincere Aloha. This project was prepared in partial satisfaction of requirements for the Honors Program, University of Hawaii, 1975. A portion of this study was presented at the Cornell University Mini-Symposium on coral reef fishes, 1976.

LITERATURE CITED

ALLEN, G. R. 1972. Anemonefishes, T.F.H. Publications, Neptune, N. J. 288 pp.

BARKLEY, R. A., B. M. ITO, and R. P. BROWN. 1964. Releases and recoveries of drift bottles and cards in the central Pacific. U.S. Fish Wildl. Serv. Spec. Sci. Rep. 492.

BARLOW, G. W. 1975. On the sociobiology of some hermaphroditic serranid fishes, the Hamlets, in Puerto Rico. Mar. Biol. 33:295–300.

BAUER, J. A., and G. KLAY. 1974. Pygmy angels spawn. Octupus 1:5.

BREDER, C. M., and D. E. ROSEN. 1966. Modes of reproduction in fishes. Natural History Press, New York. 941 pp.

BURGESS, W. E. 1974. Evidence for the elevation to family status of the angelfishes (Pomacanthidae), previously considered to be a subfamily of the butterflyfish family, Chaetodontidae. Pac. Sci. 28:57–71.

CHAVE, E. H., and D. B. ECKERT. 1974. Ecological aspects of the distribution of fishes at Fanning Island. Pac. Sci. 28:297–317.

CLARKE, T. A. 1970. Territorial behavior and population dynamics of a pomaceateid fish, the Garibaldi, *Hypsypops rubicuada*. Ecol. Mongr. 40:189–212.

COLLETTE, B. B., and F. H. TALBOT. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal–diurnal changeover. Nat. Hist. Mus. Los Ang. City Sci. Bull. 14:98–124.

DAVIS, W. P., and R. S. BIRDSONG. 1973. Coral reef fishes which forage in the water column. Helgoländer wiss. Meersunters. 24:292–306.

DOMM, S. B., and A. J. DOMM. 1973. The sequence of apearance at dawn and disappearance at dusk of some coral reef fishes. Pac. Sci. 27:128–135.

FREIHOFER, W. C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull. 8:81–189.

GOSLINE, W. A. 1958. The nature and evolution of the Hawaiian inshore fish fauna. Proc. Eighth Pac. Sci. Congr. 3:347–357.

———. 1968. Considerations regarding the evolution of Hawaiian animals. Pac. Sci. 22:267–273.

GOSLINE, W. A., and V. E. BROCK. 1960. Handbook of Hawaiian fishes. University of Hawaii Press, Honolulu. 378 pp.

HELFRICH, P. 1958. The early life history and reproductive behavior of the Maomao, *Abudefduf abdominalis* (Quoy and Gaimard). Ph.D. Thesis. University of Hawaii, Honolulu.

HOBSON, E. S. 1965. Diurnal–nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291–302.

———. 1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73. 92 pp.

———. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. U.S. 70:715–740.

———. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. U.S. 72:915–1031.

HOBSON, E. S., and J. R. CHESS. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull. U.S. 74:567–598.

JONES, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica 4: 309–361.

KORRINGA, P. 1947. The moon and periodicity in breeding marine animals. Ecol. Monogr. 17:349–381.

LEARY, D. F., G. I. MURRHY, and M. MILLER. 1975. Fecundity and length at first spawn-

ing of the Hawaiian anchovy, or Nehu (*Stolephorus purpureus* Fowler) in Kaneohe Bay, Oahu. Pac. Sci. 29:171–180.

LOBEL, P. S. 1975. Hawaiian angelfishes. Marine Aquarist 4:30–41.

LOBEL, P. S., and R. E. JOHANNES. 1977. Nesting behavior and larvae of triggerfish (Balistidae). Manuscript.

LOBEL, P. S., and M. L. REAKA. 1977. Synchronization of reproduction with seasonal currents as a mechanism for endemism in Hawaiian marine fauna. Manuscript.

MEYER, K. A. 1977. Reproductive behavior and patterns of sexuality in the Japanese labrid fish *Thalassoma cupido*. Jap. J. Ichthy. 24:101–112.

MOYER, J. T. 1975. Reproductive behavior of the damselfish *Pomacentrus nagasakiensis* at Miyake-jima, Japan. Jap. J. Ichthy. 22:151–163.

MOYER, J. T., and L. J. BELL. 1976. Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. Jap. J. Ichthy. 23:23–32.

MUNRO, J. L., V. C. GAUT, R. THOMPSON, and P. H. REESON. 1973. The spawning seasons of Caribbean reef fishes. J. Fish. Biol. 5:69–84.

MUNZ, F. W., and W. N. MCFARLAND. 1973. The significance of spectral position in the rhodopsins of tropical marine fishes. Vision Res. 13:1829–1874.

MYRBERG, A. A., JR., B. D. BRAHY, and A. R. EMERY. 1967. Field observations on reproduction of the damselfish, *Chromis multilineata* (Pomacentridae), with additional notes on general behavior. Copeia 1967: 819–827.

PILLSBURY, R. W. 1957. Avoidance of poisonous eggs of the marine fish, *Scorpaenichthys marmoratus*, by predators. Copeia 1957: 251–252.

POTTS, G. W. 1974. The coloration and its behavioral significance in the corkwing wrasse, *Crenilabrus melops*. J. Mar. Biol. Assoc. 54:925–938.

RALSTON, S. V. D. 1975. Aspects of the age and growth, reproduction and diet of the millet-seed butterflyfish *Chaetodon miliaris* (Pisces: Chaetodontidae), a Hawaiian endemic. M.S. Thesis. University of Hawaii, Honolulu. 102 pp.

———. 1976. Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths. Fish. Bull. U.S. 74:990–994.

RANDALL, J. E. 1961*a*. A contribution to the biology of the convict surgeonfish of the Hawaiian Island, *Acanthurus triostegus sandvicensis*. Pac. Sci. 15:215–271.

———. 1961*b*. Observations on the spawning of surgeonfishes (Acanthuridae) in the Society Islands. Copeia 1961:237–238.

———. 1976. The endemic shore fishes of the Hawaiian Islands, Lord Howe Island and Easter Island. Colloque Commerson 1973, O.R.S.T.O.M. Travaux et Documents 47:49–73.

RANDALL, J. E., and H. RANDALL. 1963. The spawning and early development of the Atlantic parrotfish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48:49–61.

REAKA, M. L. 1976. Lunar and tidal periodicity of molting and reproduction in stomatopod crustacea: a selfish herd hypothesis. Biol. Bull. 150:468–490.

REESE, E. S. 1973. Duration of residence by coral reef fishes on "home" reefs. Copeia 1973:145–149.

———. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Z. tierpsychol. 37:37–61.

REINBOTH, R. 1973. Dualistic reproductive behavior in the protogynous wrasse *Thalassoma bifasciatum* and some observations on its day–night changeover. Helgoländer wiss. Meersunters 24:174–191.

ROEDE, M. J. 1972. Color as related to size, sex, and behavior in seven Caribbean labrid fish species. Studies Fauna Curacao 42:1–264.

SALE, P. F. 1970. Distribution of larval Acanthuridae off Hawaii. Copeia 1970:765–766.

———. 1971. The reproductive behavior of the pomacentrid fish, *Chromis caeruleus*. Z. tierpsychol. 29:156–164.

———. 1974. Mechanisms of co-existence in

a guild of territorial fishes at Heron Island. Proc. Second Internat. Coral Reef Symp. 1:193–206.

———. 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337–359.

SCHROEDER, R. E. 1964. Photographing the night creatures of Alligator Reef. National Geographic Magazine 125:128–154.

SCHWASSMAN, H. O. 1971. Biological rhythms. Pages 371–416 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 6. Academic Press, New York.

STEVENSON, R. A. 1963. Life history and behavior of *Dascyllus albisella*, a pomacentrid fish. Ph.D. Thesis. University of Hawaii, Honolulu.

STRASBURG, D. W. 1953. The comparative ecology of two salarine blennies. Ph.D. Thesis. University of Hawaii, Honolulu.

SWERDLOFF, S. N. 1970. The comparative biology of two Hawaiian species of the damselfish genus *Chromis* (Pomacentridae). Ph.D. Thesis. University of Hawaii, Honolulu.

TESTER, A. L., and M. TAKATA. 1953. Contribution to the biology of the aholehole, a potential baitfish. Industrial Research Advisory Council Grant, Final Rep. 29. 54 pp.

WALTERS, C. K. 1967. Nest guarding behavior of the male Maomao, *Abudefduf abdominalis*. M.S. Thesis. University of Hawaii, Honolulu.

WATSON, W., and J. M. LEIS. 1974. Ichthyoplankton of Kaneohe Bay, Hawaii. UNIHI-Seagrant Rep. 75–01.

YOUNGBLUTH, M. J. 1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthiaophagus* Randall. Z. tierpsychol. 25:915–932.